

# B R E V I O R A

## Museum of Comparative Zoology

---

CAMBRIDGE, MASS.

DECEMBER 19, 1960

NUMBER 127

---

### NOTES ON THE CRANIAL ANATOMY OF NECROLEMUR

By

E. L. SIMONS<sup>1</sup> AND D. E. RUSSELL<sup>2</sup>

#### INTRODUCTION

The large number of well-preserved skulls of *Necrolemur antiquus* of the late Eocene Quercy phosphorites of south central France allow for much more detailed study of cranial anatomy in this primate than is possible for most early members of the order. In spite of the fact that cranial osteology can be studied in great detail, views as to the taxonomic position of this primate, and of the allied genera *Microchocrus*, *Nannopithec*, and *Pseudoloris* show considerable variance.

Although not all of the same provenance, little dental variability is evidenced in specimens of *Necrolemur antiquus* examined by us. In the course of this study, however, a number of differences in position and size of basicranial foramina have been observed, which are in line with mutability of cranial foramina (in individuals of the same species) reported by other authors (see Edinger and Kitts, 1954). Also, in *Necrolemur* the probability remains that known specimens differ considerably in age (from early Bartonian to late Ludian provincial ages, at least), but locality data are inadequate for precise age determinations. Comparison of upper dentitions in the M.C.Z. and Paris skulls has failed to show any dental basis for species distinctions among them.

To date, the most detailed studies of the cranium of *Necrolemur* have been by Stehlin (1916) and by Hürzeler (1948). Stehlin's thorough and excellent description can scarcely be improved on,

<sup>1</sup>Zoological Laboratories, University of Pennsylvania.

<sup>2</sup>Muséum National d'Histoire Naturelle, Paris.

but copies of this work are not as generally available as could be wished. Also, the implications of some of his early observations seem to have been neglected in later literature. In some rather significant points, recent examination of more and different skulls permits comments supplementary to his work.

### ACKNOWLEDGEMENTS

The authors would like to take this opportunity to thank Drs. J.-P. Lehman, Curator of Fossil Vertebrates at the Muséum National d'Histoire Naturelle in Paris, and A. S. Romer of the Museum of Comparative Zoology at Harvard for generously giving permission to publish on the specimens in their respective charges. Preparation of the figures, by Miss Ellen Cole, was supported by a grant from the Wenner-Gren Foundation for Anthropological Research.

### ABBREVIATIONS

In the absence of specimen numbers, the Paris Museum skulls of *Necrolemur* have been numbered 1 through 5 for convenience of reference. Abbreviations used in this paper are as follows: M.C.Z., Museum of Comparative Zoology at Harvard College. Montauban, Natural History Museum (Geological Collection), Montauban, France. Paris, National Museum of Natural History, Paris.

### CRANIAL CHARACTERS

#### I. AUDITORY REGION

Most of the information, published to date, regarding the components of the auditory bulla in *Necrolemur* comes from Montauban 9, which has been discussed by both Stehlin and Hürzeler. Even though this skull was prepared with considerable skill, the crystalline calcite filling was apparently confused with the very similar appearing bone in the region of the epitympanic recess. Consequently, the route of the stapedia artery across the tympanic cavity of the middle ear was lost just anterior to the fenestra ovalis. The extrapetrous portion of the Fallopian aqueduct was lost as well. Preparation of Paris 2 has revealed more details of the epitympanic region (Fig. 1).

Exposure of the inside of the bulla in Paris 2 and 5 indicated primarily the lack of a free annular tympanic ring. Moreover, studies by Simons (in press) on a specimen of *Necrolemur* at the

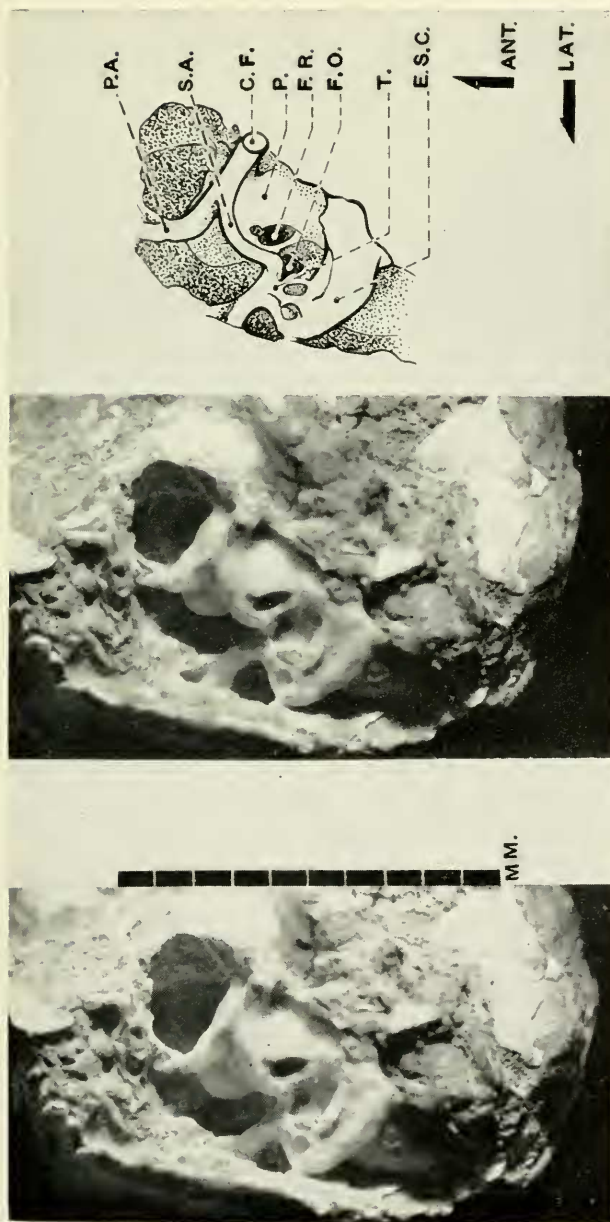


FIGURE 1

*Necrolemur antiquus*, Paris 2, interior of right bulla, x 5. Stereoscopic depth exaggerated.

Abbreviations: P.A., promontory artery; S.A., stapedial artery; C.F., carotid foramen; P., fenestra rotunda; F.O., fenestra ovalis; T., "T" of extrapetrous portion of Fallopian aqueduct; E.S.C., external semicircular canal.

British Museum (Natural History) demonstrate that the ectotympanic element is tubular, and medially fused to the ventral bulla wall. Hürzeler's evidence (1946:353; 1948:28) of the presence of a free ring, therefore, can no longer be accepted. The bone he identified as such had to be removed during preparation to expose the carotid canal and thus cannot be re-examined. In M.C.Z. 8879 the meatal tubes are reasonably well preserved but one of the Paris skulls shows an even more complete osseous meatus. Together, these indicate that the ectotympanic (external to the bulla) is about as long as the transverse diameter of the foramen magnum, curves slightly backward, and may be broadest at the external aperture. None of the fossil or recent Lemuroidea have this sort of meatus.

Hürzeler (1948:27) cites M.C.Z. 8879 as not showing any evidence of a fused tympanic ring. Nevertheless, four and possibly more transverse struts are exposed on the ventrolateral face of the right bulla of the Harvard skull. These bars are supports for the internal rim of the tubular ectotympanic.

Also of interest is the fact that the anterior route of the promontory artery (true entocarotid) is apparently variable. In Montauban 9, it curves sharply anteromedially shortly after leaving the promontory of the petrosal. In Paris 2, this curving is much less accentuated. Some crushing is to be allowed for in the tympanic region of the latter specimen but the amount of curvature illustrated by Hürzeler (1948, figs. 30 and 31) for Montauban 9 is not indicated in the Paris skull. It should be further noted that this bony tube does not lie in a horizontal plane in Montauban 9 and Paris 2, but slopes anterodorsally at an angle of about  $45^{\circ}$ .

The stapedia artery, like the promontory artery, remained enclosed in a bony tube throughout its route within the bulla. Branching from the promontory artery just inside the carotid foramen, the stapedia artery curved dorsally, lying on and following the form of the petrosal promontory. It then passed anterior to the fenestra rotunda to the bottom of the fenestra ovalis. There it diverged laterally, crossing the fenestra ovalis, and continued anteriorly nearly parallel to the promontory artery (Fig. 1). The groove mentioned by Hürzeler (1948:31) is surely a remnant of the stapedia tube, as he suggested. The exit of the stapedia artery appears to be at the dorsoanterior base of the external auditory meatus.

The extrapetrous portion of the Fallopian aqueduct is also enclosed up to, or nearly up to, its exit at the stylomastoid foramen. Its route lies lateral to the fenestra ovalis, just above the stapedial artery and continues posteriorly under the external semicircular canal. At this point, the tube forms a "T" giving rise to the small anterolateral opening and a larger posteromedian branch. The former is a natural foramen. Damage to the latter region makes it impossible to say whether or not the more posterior branch continued as an enclosed tube to the stylomastoid foramen. In Paris 2, this foramen is single, in Paris 1, double. Without exposing the interior of the bulla in Paris 1 a possible connection between the branching Fallopian aqueduct and the double stylomastoid opening cannot be confirmed. That the anterolateral foramen of the "T" in Paris 2 could have given passage to the chorda tympani seems likely.

Regarding the foramen designated FX, "Foramen von unbekannter Bedeutung," by Hürzeler (1948:fig. 28), it seems probable that this represents the opening of the inferior petrous sinus, as originally stated by Stehlin (1916:1355).

Contrary to the views of a few students, we find little distinction between *Tarsius* and *Necrolemur* in the major carotid relationships, both inside and outside the bulla. The two genera appear to agree in those features of the carotid circulation which distinguish tarsiers from Malagasy lemurs, adapids and lorises (see Le Gros Clark, 1959:151). Location of the internal carotid foramen in *Tarsius* on the ventral surface of the bulla (instead of on the median wall) constitutes a slight difference from *Necrolemur*, but it should be stressed that placement of this foramen in the fossil species does approximate the situation in *Tarsius*, being more ventral than in most, if not all, other prosimians. Furthermore, *Necrolemur* and *Tarsius* are alike in having both stapedial and promontory branches within the bulla, encased in bony canals or tubes, with the promontory division the larger. In typical Lemuriformes (Malagasy lemurs, adapines and notharetnes), the carotid foramen has a quite different location at the posteroexternal angle of the bulla and, inside it, the promontory division is very small (Gregory, 1920:174-180). Lorises and the cheirogaleine lemurs differ also, in that the carotid divides outside the entotympanic and the main branch enters the skull through the foramen lacerum medium instead of going through the bulla. A middle lacerate foramen is not present in *Tarsius* and *Necrolemur*. The few differences between these two genera to be observed in the auditory region

seem best understood with reference to the effects of the anterior shifting of the foramen magnum and greater inflation of the anterointernal part of the bulla in *Tarsius*. Some primitive features are also to be seen in the Eocene form. For instance, the canal for the promontory artery in *Necrolemur* is only slightly thicker than that for the stapedia. In *Tarsius* this difference is more pronounced. What is of general significance is that when *Necrolemur* differs from *Tarsius* it is usually intermediate between the latter and yet more primitive prosimians. One could hardly expect an Eocene tarsiod to be otherwise.

## II. BASICRANIUM

Stehlin (1916:1351) mentioned that the alisphenoids participated in the composition of the anterior wall of the bulla. However, Hürzeler (1948:26) has pointed out that, although the bulla is overlapped by the alisphenoids, this does not permit the definite statement that the alisphenoids constitute a part of the true bulla wall. In Montauban 9, it is possible to follow the suture between the bulla and its neighboring elements from the carotid foramen around the anterior end to the squamosal. The diverticulum D 2 (of Hürzeler) appears to lie outside this suture. If then, as Hürzeler suggested, the alisphenoid forms no part of the anterior bulla wall, this diverticulum (D 2) is extra-bullar. The broad overlapping of the external pterygoid plate of the alisphenoid onto the anterolateral bulla wall in *Necrolemur* (Fig. 2) is a feature of some interest in relating the Quercy form to the modern *Tarsius*. Cope (1885:467) long ago stressed the distinctiveness of this region of the tarsier basiscranium when comparing it with the then newly discovered skull of an American Wasatchian prosimian, *Tetonius homunculus*. In both *Necrolemur* and *Tetonius* these external pterygoid plates overlap the bullae, as in *Tarsius*. Gregory (1920:227) gives the following as a general character of lemuroid Primates: "The elongate pterygoid plates of the alisphenoids extended back to the auditory bullae, whereas in the Anthropeidea they are well separated from them." A further distinction here is possible in that the posterior extremities of the external pterygoid plates in lemurs and lorises, including such fossil forms as *Smilodectes*, *Notharctus*, *Adapis*, and *Pronycticebus*, typically (although not in all cases) reach back to the anterior tip of the bulla, but the area of contact is very small and cannot be described as overlapping. *Necrolemur*, *Tarsius*, and *Tetonius* differ in this respect



from lemuriform, loriform, platyrrhine, and catarrhine Primates.

Stehlin could not find the stylomastoid foramen in his specimens: Hürzeler (1948) shows it in figures 27 and 28 at the posteroexternal angle of the bulla, but does not label it (see Fig. 1). Just anterior to this foramen is a fossette, probably for reception of the stylohyal, if, as in *Tarsius*, the tympanohyal was not distinct (van der Klaauw, 1931:239). This foramen and fossette lie in the same depression and have a somewhat variable degree of separation. In M.C.Z. 8879 the external appearance is as a single oblong foramen, while in Paris 1 the two are more distinctly set off (Fig. 2). A specimen at the British Museum is intermediate in this regard.

Contrary to Stehlin's suggestion (1916:1348) that a true postglenoid process does not exist in *Necrolemur*, Paris 1 and 5 exhibit a process that can justly be termed postglenoid. Also a postglenoid foramen is present (M.C.Z. 8879, Paris 1, 2 and 5) median to this process and between the posterior limit of the glenoid area and the external auditory tube.

Two large foramina, one on either side of the alisphenoid pterygoid wing, were described by Stehlin (1916:1353-1354) as the inner and outer openings of the canalis civinninii (or foramen pterygospinosum, Stehlin 1912:1205). He named a smaller opening situated anterodorsally in the same region the foramen ovale. The position of this latter small foramen is variable, but is always anterior to the glenoid fossa instead of being approximately on a line with it, as is the foramen ovale in Primates generally. In those specimens in which this foramen is relatively large, a groove extends laterally and slightly posteriorly from it, which would probably not be the case if it were the foramen rotundum. Removal of matrix from Paris 1 and 2 in the region of the external pterygoid plate or wall has revealed a foramen opening directly into the cranial cavity, lying within the wall at the juncture of canals from the three foramina. Given this information, probably not known to Stehlin, we suggest that the posteroexternal foramen (outer opening of Stehlin's canalis civinninii) is the foramen ovale.

In a footnote, Stehlin (1916:1354) cited Gregory (1915:430) as confirming his identifications in the region of the foramen ovale. Gregory does this only partially, committing himself no further than to say that the foramen ovale is on the external (as opposed to the internal) side of the external pterygoid wall.

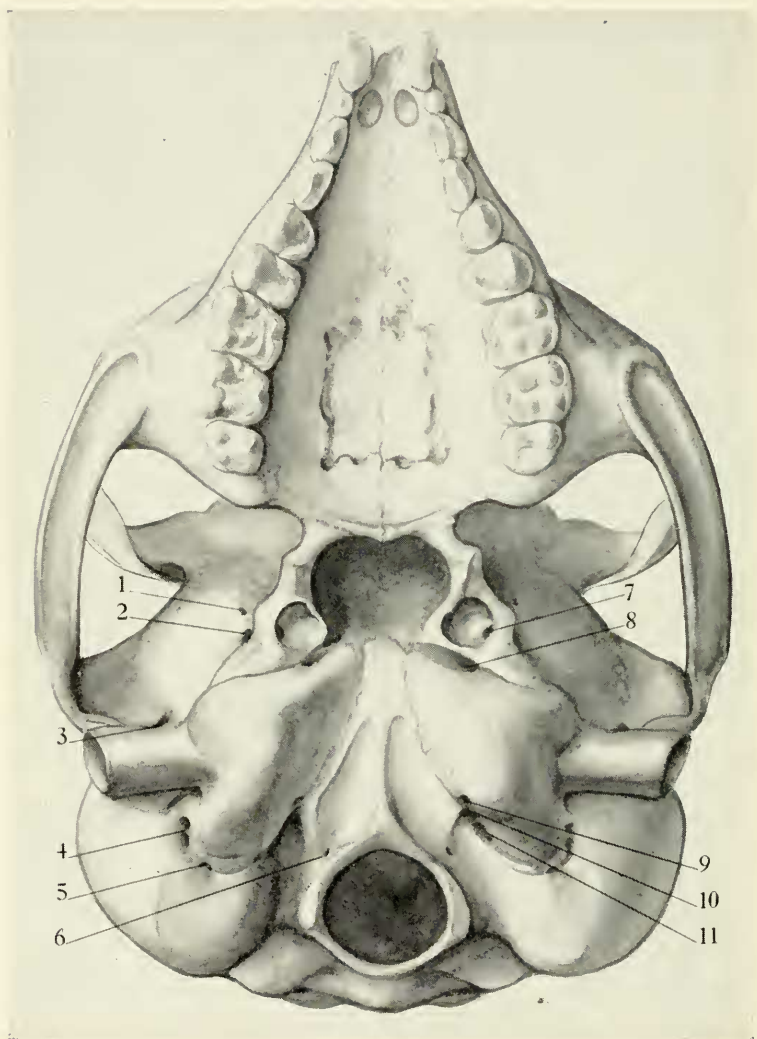


FIGURE 2

*Necrolemur antiquus* x 3.5

- |  |                                |
|--|--------------------------------|
| 1. Foramen for branch of internal maxillary artery | 6. Hypoglossal foramen         |
| 2. Foramen ovale                                   | 7. Alisphenoid canal           |
| 3. Postglenoid foramen                             | 8. Opening of eustachian tube  |
| 4. Stylomastoid foramen and fossa for ? stylohyal  | 9. Internal carotid foramen    |
| 5. Foramen for auricular branch of pneumogastric   | 10. Inferior petrous sinus     |
|  | 11. Posterior lacerate foramen |



He did not definitely say that Stehlin's small foramen is the foramen ovale. However, he identified as the foramen rotundum the smaller foramen (Stehlin's f. ovale) regarded by us as being for the internal pterygoid branch of the internal maxillary artery.

### III. ORBIT

Along its median wall the orbit is composed principally of the frontal and the maxillary. Careful search of Paris 1 revealed no os planum present in the orbital wall (Fig. 3). The lacrymal forms a narrow band within the orbit along the anterior rim. Frontal, parietal and alisphenoid comprise the posterior wall. No anterior sutures between the small orbitosphenoid, frontal, and palatine, respectively, could be made out in Paris 1, in which this region is entirely undistorted. Only a small palatine component is present in the orbit, and this does not separate the frontal from the maxillary.

Stehlin (1916:1345) noted that his material was not adequate to allow determination of the maxillo-malar suture. This led him to suggest that the malar might reach the lacrymal. Paris 1 and 2 show that this is not the case; the maxillary makes up part of the orbital rim. When discussing the Eocene lemuroid *Notharctus*, Gregory (1920:227) remarked "... the malar if not in actual contact with the lacrymal certainly came very close to it, whereas in tarsioids and anthropoids it becomes widely separated from the lacrymal and limited to the outer side of the orbit." Consequently, *Necrolemur* resembles the higher Primates in this regard, and not the majority of prosimians other than *Tarsius*.

The absence of an ethmoid component in the rostral orbital wall of *Necrolemur* has been taken by some students as an indication of a lack of affinity between it and *Tarsius*, since in the latter the os planum is large. To the writers this distinction does not seem to have much significance. A primitive prosimian condition, where the ethmoid has no orbital plate, is retained in such forms as *Necrolemur*, *Pronycticebus*, *Smilodectes* etc., in which, perhaps, there has not been enough orbital expansion to effect an expression of this bone in the orbit by impinging on the anterior part of the interorbital septum. In *Tarsius* and some Lorisiformes the interorbital septum is very narrow — evidently an accommodation for relatively large eyes, and in both groups an os planum occurs. Moreover, only in Cheirogaleinae,

among living and fossil Lemuriformes, is the os planum present. In these small lemurs also, the occurrence of an os planum is coupled with large orbits (compared to body size) and a thin interorbital septum. For the Anthropeidea, a similar origin for

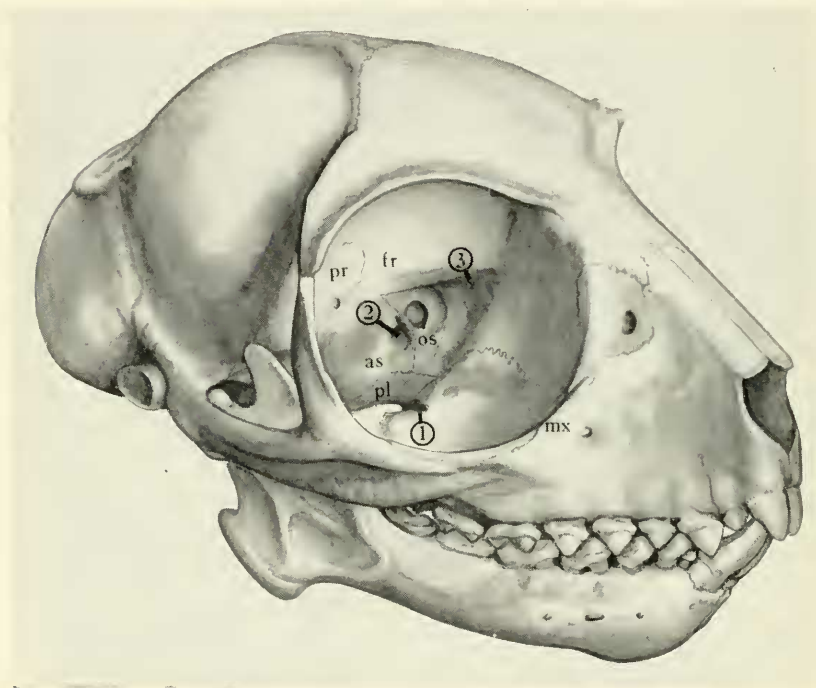


FIGURE 3

*Necrolemur antiquus* x 3.5 approx.

- |  |                    |
|--|--------------------|
| 1. Sphenopalatine foramen and posterior palatine canal         | 2. Ethmoid foramen |
| 2. Foramen rotundum and anterior lacerate foramen (?coalesced) |                    |

Abbreviations:

*as*, alisphenoid  
*fr*, frontal  
*mx*, maxilla  
*os*, orbitosphenoid  
*pl*, palatine  
*pr*, parietal

this orbital element may be considered. In most Ceboidea the orbits restrict the interorbital septum to a thin plate on which the os planum is exposed laterally. Although in Old World Anthropeidea the rostrum between the orbits is occasionally

rather broad, it is possible to posit that such breadth is secondary and that they descend in common from a form in which relatively large eyes impinged on the interorbital area enough to induce the appearance of an orbital ethmoid component. This hypothesis is strengthened by observed interorbital narrowness in the only known part of an Oligocene catarrhine skull (Simons, 1959:8). If the foregoing suggestions apply, then it is not necessary to expect the presence of an os planum in the stock from which *Tarsius* may have arisen.

In *Necrolmur* (Paris 1), a small venous foramen can be seen situated near and beneath the median dorsal rim of the orbit. As in *Tarsius*, but apparently not in other Primates, below this foramen a deep groove curves posteroventrally and (in both) lies at a juncture between the plane of the lateral wall of the rostrum and that of the back of the orbit. This is another unusual feature (occurring in both *Necrolmur* and *Tarsius*) which has to be attributed to independent acquisition, by those who doubt that any known fossil prosimians have a close phyletic relationship to *Tarsius*.

A cranio-orbital foramen exists in Paris 1, but could not be found in Paris 2, 3 or 5. Running anteroposteriorly and slightly above the optic foramen is another groove. A small opening near its anterior end appears to be the ethmoid foramen. The sphenopalatine foramen and the posterior palatine canal in Paris 1 are combined to open posteriorly through a common large foramen in the suture between maxillary and palatine.

Apparently coalescence of the foramen rotundum and the anterior lacerate foramen occurs in Paris 1 but they are separate in Paris 5. In both cases, however, the foramen rotundum lies within the orbit, as Stehlin noted (1916:1353), and not lateral to the postorbital part of the alisphenoids, as Gregory (1915:430) suggested.

The orbital region of Paris 1 is entirely undistorted and shows that the postorbital opening was small. It is of some interest that neither lemurs nor lorises, nor any other known fossil prosimians of similar size possess a smaller aperture here. As with so many cranial characters the primate showing the most interesting resemblance to *Necrolmur* in respect of the structure of the postorbital region is *Tarsius*. However, because of the huge flanges that encircle the orbit in mature specimens of *Tarsius*, and the greater degree of postorbital closure seen in such adults, much more revealing comparisons can be made between skulls of

*Necrolemur* and those of juvenile tarsiers. In the latter, the circumorbital flanges are not yet very pronounced and resemble the slight flanges seen in *Necrolemur* (Fig. 3). It seems necessary to assume, first, that these flanges in *Tarsius* are concerned primarily with the support of the enormous eyes, and second, because of their very uniqueness, that they were not so developed in Eocene forerunners of the living genus. *Necrolemur* clearly has such flanges in an incipient stage.

Closure behind the orbit in *Tarsius* (on the outside) can be seen to proceed in successively older juveniles from three main centers: 1, ventrolaterally, by an upgrowth of the posterior mid-region of the orbital plate of the maxilla; 2, laterally, by an anteroposterior spreading of the middle of the postorbital bar; and 3, dorsolaterally, by growth of a flange from the frontal, which arises beneath the frontal insertion of the postorbital bar. Ossification proceeds downward as this flange, or plate, grows alongside the postorbital bar, and it eventually fuses with the bar, leaving no sutural indication. In most specimens of adult *Tarsius*, the frontal and jugal components of the postorbital wall can be distinguished by the fact that the region where they fuse is much thinner and consequently more translucent. In *Necrolemur*, at least two of these components effecting closure appear to be partially developed. Paris 1 has an unerushed post-orbital bar which shows an anteroposterior spreading at the middle, much as in *Tarsius*. The evidence is less clear because of breakage, but the posterior part of the orbital plate of the maxilla also bears a flange in *Necrolemur*. The third center of closure seen in *Tarsius*, the frontal element, is indicated in *Necrolemur* only by a distinct angulation along the lateral wall of the cranium between the orbital and temporal fossae. Although such characters as the greatly reduced paraconids and the loss of certain anterior lower teeth eliminate *Necrolemur* from the direct ancestry of *Tarsius*<sup>1</sup>, the incipient circumorbital flanges and characteristics of postorbital closure in *Necrolemur* are suggestive of a stage to be expected in the *Tarsius* ancestry. Perhaps *Pseudoloris* or *Nannopithec* are nearer the actual line leading to the modern form, but incompleteness of known specimens prevents the sort of comparisons here made with *Necrolemur* and leaves this possibility insoluble at present.

<sup>1</sup>Even if this were not so it would be almost irrelevant, in the absence of intermediates, to urge an ancestor-descendent relationship for forms so separate in geographic distribution and in time.

It may be noted in passing, that the manner of postorbital closure in *Tarsius* (insofar as the malar and frontal are concerned) is distinct from that seen in catarrhines and platyrrhines. Closure in this area in *Tarsius* is chiefly effected by an outward and downward growth of a flange of the frontal (with relatively little malar expansion) while in higher Primates the greater part of the dorsolateral area of enclosure is contributed by the development of an orbital plate of the malar. These differences strongly imply that the partial postorbital closure of *Tarsius* only parallels that of the Anthroproidea and is not a character of their common inheritance. If it be agreed that some postorbital closure arose at least twice among Primates, the possibility that this feature also was independently acquired in the ancestral platyrrhine and catarrhine stocks can be more seriously entertained.

### EXPLANATION OF FIGURES

The lateral and ventral views of the skull of *Necrolemur* are based on Paris 1, to which details of missing regions have been added from other specimens, principally M.C.Z. 8879. Misleading stains and fractures in Paris 1 are largely omitted from these illustrations. Certain details of the anterior dentition and mandible are drawn from specimens figured by Stehlin (1916).

### REFERENCES

COPE, E. D.

1885. The Lemuroidea and the Insectivora of the Eocene period of North America. *Amer. Naturalist*, **19**: 457-471.

EDINGER, T. and D. B. KITTS

1954. The foremen ovale. *Evolution*, **8**: 389-404.

GREGORY, W. K.

1915. I. On the relationship of the Eocene lemur *Notharctus* to the Adapidae and to other Primates. II. On the classification and phylogeny of the Lemuroidea. *Bull. Geo. Soc. Amer.*, **26**: 419-446.  
1920. On the structure and relations of *Notharctus*, an American Eocene primate. *Mem. Amer. Mus. Nat. Hist.*, (n.s.) **3**: 49-243.

HÜRZELER, J.

1946. Zur Charakteristik, systematischen Stellung, Phylogenese und Verbreitung der Necrolemuriden aus dem europäischen Eocaen. *Eclogae geol. Helvetiae*, **39**: 352-354.  
1948. Zur Stammesgeschichte der Necrolemuriden. *Schweiz. paläont. Abh.*, **66**: 3-46.

KLAUW, C. J. VAN DER

1931. The auditory bulla in some fossil mammals. Bull. Amer. Mus. Nat. History., **62**: 1-352

LE GROS CLARK, W. E.

1959. The antecedents of man. 374 pp. Edinburgh University Press.

SIMONS, E. L.

1959. An anthropoid frontal bone from the Fayum Oligocene of Egypt: the oldest skull fragment of a higher primate. Amer. Mus. Novit., no. 1976: 1-16.
1960. Notes on Eocene tarsioids at the British Museum. Bull. Brit. Mus. Nat. Hist., Geol. Ser., in press.

STEHLIN, H. G.

1912. Die Säugetiere des schweizerischen Eocaens. Abh. Schweiz. Paläont. Gesell., **38**: 1165-1298.
1916. Die Säugetiere des schweizerischen Eocaens. *Ibid.*, **38**: 1299-1552.